

# A Study of the Pollination of *Alocasia macrorrhiza* (L.) G. Don (Araceae) in southeast Queensland

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Flowering of *Alocasia macrorrhiza* (L.) G. Don in southeast Queensland was investigated and appears to be protogynous. Insects in the open spathe chambers, on the spadix after closure of the constricting area, and in the sealed chamber of the nearly mature inflorescences were recorded to determine possible pollinators. The number of seed set in an experiment involving various combinations of emasculation and bagging of 143 inflorescences including controls appear to indicate cross pollination by insects.

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## INTRODUCTION

*Alocasia macrorrhiza* (L.) G. Don (Araceae) occurs in wet tropical Asia, eastern Australia and the Pacific Islands; to some of the latter at least it was probably introduced, as well as to other parts of the wet tropics and subtropics. In Australia it occurs in the high rainfall coastal areas and adjacent plateau regions in Queensland and New South Wales, from about 12° to 34°S latitude.

Hamilton (1898) reported the beetle, *Brachyepelus murrayi* Macleay (Coleoptera: Nitidulidae) as the pollinator of *A. macrorrhiza*, and that a species of Agariidae (Lepidoptera) also aids in fertilization. McAlpine (1978) described *Neurochaeta inversa* (Diptera: Neurochaetidae) (whose life cycle is intimately connected with the flowers of this plant growing in its natural habitat in eastern Australia) which he thought may act as the pollinator. He observed, however, that as many insects visit the flowers, it is probably not the sole agent.

Shaw *et al.* (1982) reported that *A. macrorrhiza* still set seed in gardens where no *N. inversa* were recorded, and in remnant natural stands now surrounded by mainly non-forested areas, where occurrence of *N. inversa* was sparse. It was also shown that seed set in plants from rainforest areas was not related to the numbers of *N. inversa* recorded in chambers of developing and matured inflorescences. They concluded, therefore, that pollination is probably independent of ovipositing females of *N. inversa*.

The present study records the stages of flowering and the insects associated with the inflorescences or flowering heads (hereafter called 'heads') and in the nearly mature inflorescences. Also reported are the results of an experiment involving emasculation and bagging of heads before anthesis, with controls, to provide information on the possibilities of selfing or crossing, and of wind or insect pollination, as measured by seed set.

## SITES AND METHODS

### *Sites*

*A. macrorrhiza* has been under study since 1980, but the work reported below was mainly carried out in the flowering period October 1981 to March 1982 in southeast

Queensland, at sites in rainforest areas along the coastal range west and southwest of Brisbane, and in simulated rainforest areas (gardens) in Brisbane suburbs. Details of the sites are as follows:

*Rainforest:* Three sites in small private holdings adjacent to large or relatively large reserved areas of rainforest at Mt Nebo, Mt Glorious and Mt Tamborine, at about 520, 650 and 500 m above sea level (a.s.l.) respectively; plants at the first and third sites were growing in and at the edge of streams; at each site plants occurred in scattered clumps.

*Garden:* Three sites in the Mt Coot-tha Botanic Gardens, developed as simulated rainforest in natural sclerophyll forest during the last four years, and one site at the University of Queensland, St Lucia, surrounded by parklands; all sites about 50 m a.s.l.; plants at one site at Mt Coot-tha and most plants at St Lucia, at the edge of streams; at each site plants occurred in scattered clumps.

#### *Methods*

At each site inflorescences were examined throughout the entire flowering period and observations made on the various stages of flowering, both in the field and on excised heads removed to the laboratory. In some in situ (non-treatment) and other excised heads, small hinged 'windows' about 1 cm square were cut into the wall of the spathal chamber for stigma viewing, the flap being resealed with adhesive tape.

All sites were visited as frequently as possible after the treatments below were applied. Any rotting heads were harvested when the rotting became evident, but heads maturing were allowed to remain in situ until near maturity but before actual splitting of the wall of the spathal chamber to ensure no seeds were lost. Each head was examined at harvest, and if any fertilization had occurred, the numbers of unfertilized ovaries, fertilized ovaries (berries) and fertilized ovules (seed) were determined.

#### *a. Treatments*

Emasculation and bagging were carried out only on 'buds' when each spadix was still enclosed by the furled spathe, prior to anthesis. The treatments were as follows:

1. *Emasculated, mesh-bagged.* This involved the excision of the distal portion of the spathe (consisting of the furled spathal limb, the sterile terminal appendage, the portion bearing the staminate flowers and the upper portion of the median sterile florets) at the constricted zone. The excised part of the spadix was removed from the excised spathal limb and checked to ensure that all the staminate flowers had been removed. The portion of the spadix remaining on the plant (consisting of the lower part of the median sterile florets and the pistillate flowers) was enclosed by a nylon mesh bag fine enough to keep out insects larger than thrips — no thrips, however, although they could physically enter, were found inside the bags.
2. *Emasculated, unbagged.* As above, but unbagged.
3. *Non-emasculated, whole head paper-bagged.* A white paper bag normally used in maize pollination studies was employed.
4. *Non-emasculated, whole head plastic-bagged.* A commercially available clear plastic bag was found to be suitable.
5. *Non-emasculated, whole head mesh-bagged.* Similar bag as used in Treatment 1. In some cases the bags were distended by the insertion of a framework composed of two metal rings maintained in position on a rigid metal upright attached to the peduncle.
6. *Non-emasculated, unbagged, labelled.* Heads untouched, labelled as controls while still in bud.

During each visit to the field, at least one set of the six above treatments were prepared, heads being labelled individually. Occasionally additional heads of some of

the treatments were included if extra heads were available. All the paper, plastic and mesh bags were tied at the base with nylon net tape.

7. *Non-emasculated, unbagged, unlabelled.* Early maturing heads at each site, previously unused in our experiments, were also harvested as further controls for comparison.

b. *Insects*

Records were made of all insects observed within the *open* spathal chamber when the pistillate flowers were exposed and those later found around the staminate flowers and on the accumulated pollen of the spathal 'catchment area' above the constricted portion at the base of the spathal limb. An aspirator was used to collect representative samples of all species of insects encountered (from non-treatment heads). Any insects in the sealed spathal chambers of treatment heads at harvest, whether immature or adult, were also recorded and retained.

## RESULTS

### *Flowering*

After the green spathal limb unfurls, the constricting portion at the base of the limb gapes widely, with a gap of 3–4 mm around the spadix, so that the pistillate flowers can be partially viewed from above. At this stage the subsessile stigmas appear dull, white and rough, and the 2–3–(4) short lobes are seen microscopically to consist of a cushion of short hyaline 'hairs' ca 138 to 227  $\mu\text{m}$  long and ca 13 to 23  $\mu\text{m}$  wide (mean 157.1 by 16.2  $\mu\text{m}$ ), to which the sticky pollen grains adhere. The chamber is open for about one day in the field, after which the constricting portion of the spathe closes tightly around the spadix in the region of the median sterile florets, sealing off the chamber. Pollen is then extruded in white cirri from the synandria of the staminate flowers for about two days, and fallen pollen accumulates in the pollen catchment area formed at the base of the spathal limb above the constriction. At this stage, stigmas in the enclosed chamber are glistening, white and glutinous. (The only exceptions noted to the above were a few heads from 650 m a.s.l., excised at the beginning of anthesis, and then held in the laboratory at about 50 m a.s.l. Some pollen in each head began to extrude, mainly from the lower staminate flowers, before the final closure of the constricting portion. This may have been because the heads had not been visited by insects, and the 'unfertilized' stigmas may have been receptive longer, perhaps delaying the closure. Also, as Stanley and Linskens (1974) pointed out, altitude and temperature affect pollen dehiscence, so that the warmer temperature in the laboratory at the lower altitude may have caused extrusion of the pollen earlier than normal. This, however, was an unnatural situation.)

A fragrance, present at the beginning of anthesis, was still present after pollen extrusion, though less pronounced.

Details of pollen studies will be published separately, but are summarized here as follows: When extruded in the cirri, the pollen is sticky and will adhere to a scalpel blade, but the stickiness decreases with age, so that accumulated pollen, although still mainly in clumps, could be launched into the air by deliberately jarring the head. In the cirri, the pollen appears white, but when shaken out of the head is deep ivory, about plate 4A2 in the Methuen Handbook of Colour (Kornerup and Wanscher, 1961). The grains are microscopically colourless, spherical, 32.3–47.5  $\mu\text{m}$  long by 30.3–47.5  $\mu\text{m}$  wide (mean 41.2  $\times$  39.3  $\mu\text{m}$ ) excluding ornamentation of surface spinules ca 2  $\mu\text{m}$  long. Twenty-two samples of pollen shaken from 10 heads, examined microscopically, revealed no pollen other than that of *A. macrorrhiza*. In germination tests on modified Brewbaker and Kwack (1973) medium, pollen shaken from heads in the laboratory at the beginning of each day was mainly viable during the first and

TABLE 1

Presence (+) or absence (-) of insects recorded in the open chambers (O) and around the spadix after sealing of the chambers (AS) of non-treatment heads

HABITAT, locality, site	<i>N. inversa</i>		<i>T. carbonaria</i>		Insects <i>Brachyepplus</i> sp.		Staphyl- inidae		<i>Taenio- thrips</i>		Other*	
	O	AS	O	AS	O	AS	O	AS	O	AS	O	AS
	RAINFOREST											
Mt Nebo	+	+	+	+	+	+	+	+	-	+	5	
Mt Glorious	+	+	+	+	+	+	+	+	-	+	2,7	
Mt Tamborine	+	+	-	-	+	+	+	+	-	+	3,5 3	
GARDEN												
Mt Coot-tha												
Site 1	+#	-	+	+	+	+	+	+	+	+	6	4
Site 2	-	-	+	+	+	+	+	+	-	+	1	
Site 3	+#	-	+	+	+	+	+	+	-	+	8	
St Lucia	-	-	-	-	+	+	+	+	-	+		

% Other = 1 *A. mellifera* #

2 Pteromalidae #

3 Curculionidae (5 specimens: 4 open chamber; 1 around spadix)

4 *P. fimetarius* #

5 *Cyphon* sp. (2 specimens)

6 *T. ? minor* #

7 *Hippelates* sp. (2 specimens)

8 Dolichopodidae #

# only single individuals

second days of production, with much lower and slower germination on the third day and only rarely on the fourth day. Some sterile (non-staining) inviable pollen was present in samples from all sites.

### Insects

#### 1. Within the open chamber

Four species of insects were commonly encountered within the open chamber (Table 1). These were *N. inversa*, *Trigona carbonaria* Smith (Hymenoptera: Apidae), *Brachyepplus* sp. (Coleoptera: Nitidulidae) and an unidentified alaocharine staphylinid (Coleoptera: Staphylinidae). The two beetles were present at all localities while *N. inversa* was limited to rainforest localities except for two specimens (only one captured) at Mt Coot-tha. Although common at most localities, *T. carbonaria* was not recorded during any visit to Mt Tamborine or St Lucia.

Several other insects were occasionally recorded within open spathe chambers, but usually only as single individuals. These were *Taeniothrips (Isochaetothrips)* sp. (Thysanoptera: Thripidae), *Cyphon* sp. (Coleoptera: Scirtidae), *Triphyllus ?minor* Lea (Coleoptera: Mycetophagidae), an unidentified derelomine weevil (Coleoptera: Curculionidae), *Hippelates* sp. (Diptera: Chloropidae), an unidentified dolichopodid (Diptera: Dolichopodidae) and an unidentified pteromalid (Hymenoptera: Pteromalidae) (Table 1).

#### 2. On the spadix after closure of the constricting portion

Four species of insects were commonly encountered on the spadix (or in the accumulated pollen) after closure of the spathe constriction. These were *T. carbonaria*, *Brachyepplus* sp., the staphylinid and *Taeniothrips (Isochaetothrips)* sp. All were present at each locality except for *T. carbonaria* which was absent as noted previously (Table 1).

TABLE 2

*Insects other than Neurochaeta inversa recorded in sealed chambers of matured heads\**

HABITAT, locality	Head designation	<i>Brachyepelus</i> sp. No.	Chloro- pidae No.	Insects*			
				Muscidae No.	Diptera unidentified No.	Formi- cidae No.	Collem- bola No.
RAINFOREST							
Mt Nebo	7A.4		2 L				
			2 P				
Mt Glorious	6A.1		1 L#				
	X.1	1 L					
	X.2	1 L					
Mt Tamborine	1A.1	1 L					
	1A.4				2 L		
	9A.1	1 L					
	9A.2	1 L					
	X.1			1 A			
	X.2	6 P	1 L				
	X.4	1 A	1 P			2 A =	
		2 L					
GARDEN							
Mt Coot-tha							
Site 2	1A.1						1 L

\* Chambers in 131 observed heads (including unlabelled controls) were without insects, other than presence of *N. inversa* in some.

\* Life forms: L = larva; P = pupa or puparium; A = adult.

# Larvae in one of two damaged ovaries.

= Dead.

TABLE 3

*Numbers and fate of heads in seven treatments*

HABITAT, locality, site	Heads in the following classes													
	Emasculated						Non-emasculated							
	Mesh- bagged		Unbagged		Paper- bagged		Plastic- bagged		Mesh- bagged		Unbagged, labelled		Unbagged, unlabelled	
	M	R	M	R	M	R	M	R	M	R	M	R	M	R
No. No. No. No. No. No. No. No. No. No. No. No. No. No.														
RAINFOREST														
Mt Nebo			0	1			0	1			4	0	2	x
Mt Glorious	0	5	1	2	0	2	0	3	0	7	2	3	3	
Mt Tamborine	0	6	0	6	0	2	0	4	0	5	4	1	8	x
GARDEN														
Mt Coot-tha														
Site 1	0	3	0	3	0	2	0	3	1	2	3	1	2	x
Site 2	0	3	2	1	0	3	0	2	0	3	3	1	1	x
Site 3	0	1	0	2	0	5	0	3	0	1	3	1	3	x
St Lucia			0	3	0	1	0	3			4	0	2	x
Total	0	18	3	18	0	15	0	19	1	18	23	7	21	x

M = Matured; all heads with seed (details Table 4)

R = Rotted; all heads without seed except four with few seeds (details Table 4)

x = Some rotted heads occurring naturally, but uncounted.

TABLE 4

*Numbers of seed set in treated heads*

HABITAT, locality, site	Heads in the following classes						
	Emasculated				Non-emasculated		
	Mesh- bagged No.	Unbagged No.	Paper- bagged No.	Plastic- bagged No.	Mesh- bagged No.	Unbagged, labelled No.	Unbagged, unlabelled No.
RAINFOREST							
Mt Nebo		6*		0		66 229 191 260	310 381
Mt Glorious	0 0 0 0 0	37 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0 0	0 0 2* 148 138	131 140 103
Mt Tamborine	0 0 0 0 0 0	0 0 0 0 0 0	0 0 0 0 0 0	2* 0 0 0 0 0	5* 0 0 0 0 0	33 69 152 41 0	223 183 434 180 147 5 64 101
GARDEN							
Mt Coot-tha							
Site 1	0 0 0	0 0 0	0 0 0	0 0 0	13 0 0	174 0 130 173	205 106
Site 2	0 0 0	173 12 0	0 0 0	0 0 0	0 0 0	223 0 6 44	137
Site 3	0	0 0	0 0 0 0	0 0 0 0	0 0 0	173 155 0 14	109 18 98
St Lucia		0 0 0	0	0 0 0		101 137 288 44	2 40
Total heads, No.	18	21	15	19	19	30	21
Total seeds, No.	0	228	0	2	18	2649	3117
Seed, Mean	0	10.9	0	0.1	0.9	88.3	148.4

\* Heads rotted, although a few seeds were set.

Occasional encounters were *Apis mellifera* L. (Hymenoptera: Apidae), *N. inversa*, *Phalacrus fimetarius* (F.) (Coleoptera: Phalacridae) and the unidentified weevil (Table 1).

### 3. Within the sealed spathal chamber near maturity

The main species found within the sealed spathal chambers near maturity was *N. inversa*, as recorded in Table 5. It occurred, however, only at the rainforest sites, not in the gardens. A few occasional insects were also recorded, as listed in Table 2.

#### *Inflorescence treatments*

In all, 139 heads were involved in Treatments 1 to 6. Of these, 10 were lost through accident, stealth, etc., and seven heads in Treatment 3 were discarded because of perforation of the paper bags due to heavy rainfall and possibly pressure from the growing heads, giving an actual total of 122 heads. In addition, 21 heads in Treatment 7 were included in the results for comparison, making a total of 143 heads.

The results are reported in Tables 3 to 6. Table 3 shows the number of heads maturing or rotting for each treatment. No difference in behaviour occurred between any site, locality or habitat, nor was any difference noted between heads bagged with paper bags compared with those with plastic bags. Some rotted heads occurred naturally, as shown in the labelled and unlabelled controls. Only those heads matured where seed had set except for four, which between them had only 12 berries with 15 seeds. Conversely, the only heads which rotted were those where no seed had set, apart from the four exceptions mentioned previously.

The details of seed set are given in Table 4. The only heads which set seed were those of the controls, except for four unbagged, emasculated heads (one of which rotted) and one plastic-bagged and two mesh-bagged non-emasculated heads (two of which rotted).

Table 5 shows the numbers of fertilized ovaries (berries) and fertilized ovules (seed) for all matured heads and the numbers (or absence) of *N. inversa* (mainly puparia) recorded in the sealed chambers of these heads. Seed set varied considerably at most sites, ranging from 1.5% (St Lucia) to 99.3% (Mt Nebo). The numbers of *N. inversa* per head ranged from three (Mt Tamborine) to 77 (Mt Glorious) with averages of 24.2, 26.5 and 17.5 respectively for the three rainforest localities (Mt Nebo, Mt Glorious and Mt Tamborine). There was no relation between numbers of *N. inversa* and the numbers of seed set per head, locality or habitat. No *N. inversa* were recorded in heads from the garden areas, but up to 88.3% of seed was still set.

## DISCUSSION

### *Pollination ecology*

In *A. macrorrhiza* the pistils (megasporophylls) and stamens (microsporophylls) are present on different parts of the flowering head of the same plant. The exposure of the stigmas by gaping of the constricting areas at the unfurling of the spathal limb, presumably at the time of receptivity of the stigmatic surface, and the closing of the constricting portion of the spathe (therefore isolating the pistillate flowers) before the extrusion of the pollen, indicate protogyny. The precise period and peak of stigma receptivity, measured by the number and maximum of seeds set, need to be determined by controlled crossing at different times during anthesis.

The possibility of pollination by wind (anemophily) as against insect pollination (entomophily) is examined below.

The pollen when first extruded in cirri above the surface of the staminate flowers (and in the best position for pick-up by wind currents) is at its stickiest and so less likely to be wind dispersed. Also, the extended, upright and slightly incurved spathal limb would act as a protector and deflector of wind from the rear of the head. After the

TABLE 5

*Numbers and percentages of fertilized ovaries (berries) and numbers of seed and N. inversa per head, locality and habitat for all matured heads*

HABITAT, locality, head designation	Fertilized ovaries (berries) per head		Seed per head			<i>N. inversa</i> per head		
	No.	%	No.	Locality Mean	Habitat Mean	No.	Locality Mean	Habitat Mean
RAINFOREST					156.9			21.4
Mt Nebo				239.5			24.2	
6A.1	55	49.1	66			21		
6A.2	131	89.1	229			26		
7A.1	124	72.9	191			46		
7A.2	107	76.4	260			11		
X.1	150	95.5	310			16		
X.2	149	99.3	381			25		
Mt Glorious				116.2			26.5	
6A.1	87	58.8	148			11		
6A.2	88	59.9	138			8		
X.1	128	75.7	131			22		
X.2	140	97.2	140			11		
X.3	134	61.9	103			77		
8B	26	24.1	37			30		
Mt Tamborine				136.0			17.5	
1A.1	29	22.3	33			3		
1A.4	46	28.9	69			29		
9A.1	117	92.1	152			7		
9A.2	32	23.5	41			18		
X.1	145	72.5	223			12		
X.2	117	46.3	183			19		
X.3	210	98.1	434			31		
X.4	85	61.6	180			6		
X.5	96	49.0	147			29		
X.6	5	2.9	5			9		
X.7	47	44.8	64			20		
X.8	69	47.9	101			27		
GARDEN					107.3			0
Mt Coot-tha				133.5			0	
Site 1								
1A	132	60.6	174			0		
5A.1	80	63.5	130			0		
5A.2	145	87.9	173			0		
X.1	136	88.3	205			0		
X.2	77	43.5	106			0		
1D	10	6.5	13			0		
Site 2				99.2			0	
1A	143	77.3	223			0		
4A.1	6	5.3	6			0		
4A.2	33	56.9	44			0		
X.1	117	83.0	137			0		
1B	155	74.9	173			0		
4B	10	5.8	12			0		
Site 3				94.5			0	
1A.1	92	52.0	173			0		
1A.2	119	58.3	155			0		



5A	10	7.6	14	0
X.1	62	30.7	109	0
X.2	14	8.6	18	0
X.3	75	42.9	98	0
St Lucia			102.0	0
3A.1	71	38.0	101	0
3A.2	127	72.2	137	0
3A.3	151	77.4	288	0
3A.4	24	19.5	44	0
X.1	2	1.5	2	0
X.2	32	14.1	40	0

TABLE 6

*Theoretical expectancies of selfing vs crossing and wind vs insect pollination and the actual results*

Mechanism	Heads in the following classes				
	Emasculated		Non-emasculated		
	Mesh-bagged	Unbagged	Paper- and plastic-bagged	Mesh-bagged	Unbagged
SELFED <sup>1</sup>	no seed	no seed	seed	seed	seed
CROSSED					
<i>Wind</i>					
Pollen reaching chamber of emasculated heads <sup>2</sup>	seed	seed	no seed	seed	seed
Pollen not reaching chamber of emasculated heads <sup>2</sup>	no seed	no seed	no seed	seed	seed
<i>Insects</i>					
Attractant still present in emasculated heads <sup>3</sup>	no seed	seed	no seed	no seed	seed
Attractant excised in emasculated heads <sup>3</sup>	no seed	no seed	no seed	no seed	seed
<i>If insect crossed, attractant excised, no. of heads with:</i> (Theoretical)					
Seed	0	0	0	0	30
No seed	18	21	34	19	0
(Actual)					
Seed	0	4	1 (2 seeds)	2 (few seeds)	24
No seed	18	17	33	17	6

<sup>1</sup> Normally protogynous, but selfing is perhaps possible in absence of cross pollen or pollinator(s) if some residual stigma receptivity is still present at time of pollen extrusion, unless self-incompatible.

<sup>2</sup> Cross pollen would need to find the small entrance to the spathal chamber.

<sup>3</sup> Attractant (possibly fragrance) probably situated in the appendage/staminate portion of the spadix removed with emasculation.

pollen has fallen, when it is less sticky, the grains are fairly well protected from wind pick-up, being within the overlap at the base of the spathal limb in front (in the pollen catchment area) and the spadix itself at the back. However, neither occurrence (that is, stickiness when extruded and protection within the base of the overlapping spathal limb) need necessarily completely exclude the possibility of dispersal of some pollen

grains by wind. This may occur, as previously reported, by deliberately jarring the head. Such jarring could occur in nature by falling branches, accidental encounters by birds or ground animals and possibly by high winds.

Faegri and Pijl (1979) have stated that an obvious condition for effective wind pollination is the presence of wind, as found in open, sparse vegetation or in the top layer of closed, multi-layered vegetation types, and that in dense forest vegetation wind is so slight and infrequent that anemophily is contra-indicated. At all the sites except Site 3 at Mt Coot-tha the plants under study were part of the understorey, and at most sites were well protected by topography (being in or on the banks of streams) and by lush gully vegetation.

Provided pollen grains are fortuitously distributed, the total output of pollen produced,  $N$ , gives a number of 'effective' grains, i.e. grains carrying out pollination,  $n$ , which is a function of the areas of stigmatic surfaces,  $a$ , and the total area of the surroundings,  $A$ :  $\frac{n}{N} \sim \frac{a}{A}$  (Faegri and Pijl, 1979). The production of inflorescences on

any plant of *A. macrorrhiza* is sequential, so that when a head is in anthesis, the previous head is already in 'pod' (with the spathal chamber sealed) and the subsequent head is still in bud, with the spathe still furled. Therefore pollen, if wind-borne, would need to encounter heads on other plants at the right stage of stigma receptivity. Such heads could occur on plants in neighbouring clumps, though these are often scattered and sparse. Wind pollination is considered much less precise than biotic pollination, and to achieve its objective it presumes a very high incidence of pollen grains near their source, the dilution factor going by a power of 3 of the distance (Faegri and Pijl, 1979). While considerable pollen of *A. macrorrhiza* is produced in any one head, the overall quantity in any one area would not be great, and also it is either sticky when at source or when older and less sticky is protected from easy wind pick-up in the pollen catchment area, as discussed previously. Even if wind-borne pollen were to encounter a recently unfurled head with receptive stigmas, the pollen has to reach those receptive surfaces. The chance of wind-borne pollen falling under gravity directly into an open chamber through the gaping constricting area would seem rather remote. Alternatively, wind-borne grains could strike the inner surface of the extended upright spathal limb, if the limb happened to be at an appropriate angle to the line of flight, but again the grains would need to fall directly, or down the side of the spathal limb, onto a receptive surface. Even if a successful landing on a receptive stigma (pollination) was achieved, successful fertilization (germination on the stigma and fertilization of the ovules) may not necessarily follow, because the less sticky pollen and therefore more readily available for wind dispersal, the older and less viable it is, and therefore less capable of achieving germination and fertilization.

Faegri and Pijl (1979) pointed out that one of the factors of major importance in anemophiles is the buoyancy of the pollen grains, which increases as the size of the grain decreases, and considered that pollen of anemophiles belongs to the smaller size classes with a 'typical' diameter of 20–30–(60)  $\mu\text{m}$ , even if equally small or even smaller pollen grains are found in many entomophiles. Contributing to the effectivity of pollen transport in anemophiles and to the buoyancy of the pollen is the fact that grains do not adhere to each other, but are smooth and dry and are spread separately or in very small groups. Entomophilous pollen, on the other hand, is ornamented and sticky and the grains stick together (Faegri and Pijl, 1979). Thus the size of *A. macrorrhiza* pollen (mean  $41.2 \times 39.3 \mu\text{m}$  exclusive of ornamentation) measured in this study is in the larger part of the range for an anemophile, and their ornamentation of spinules and their stickiness suggest an entomophile.

In *A. macrorrhiza* therefore, the extrusion of sticky pollen in cirri, the continued

though decreased stickiness of the pollen with age, coupled with decrease in viability, the occurrence of spinules on the pollen grains and the short stigmatic hairs all suggest pollination by insects (entomophily) rather than wind pollination (anemophily). In addition, the occurrence of the fragrance at anthesis may also indicate entomophily.

#### *Insects*

*N. inversa* was present in all open chambers (Table 1) examined from the rainforest localities, usually moving on the walls of the chamber, seldom near the stigmas. Flies were seldom encountered on the spadix, either before or after closure of the spathal constriction, and were much more often seen running over the spathal limb. On three occasions copulating pairs were noted, once within an open chamber and twice on the inside face of the spathal limb.

*Brachypeplus* sp. and the aleocharine staphylinid were usually moving over the ovaries below the stigmas in open chambers. No beetles, when examined microscopically, had pollen adhering, but this could have been dislodged during capture. *T. carbonaria* collected from the open chambers were from the stigmas, often with heavy pollen loads in their corbiculae. Macroscopically the corbicular pellets appeared homogeneous in colour and texture. Microscopical examination of samples from six pellets chosen at random showed that they were entirely composed of *A. macrorrhiza* pollen, except for four foreign grains from one sample. *T. carbonaria* was therefore mainly '*A. macrorrhiza* constant' and must be considered to be a possible pollinating agent since they were also often observed collecting pollen on heads with sealed chambers.

Of the insects occasionally recorded within the open chambers (Table 1) the thrips were present in large numbers on the spadix of such inflorescences at all localities and the presence of some in the chamber would be expected. The records of the remaining species cannot be easily explained but is probably due to chance occurrence. In any case, their rarity discounts any possibility of their being effective pollinators.

Considering the insects on the exposed spadix after closure of the spathal constriction (Table 1), *T. carbonaria* were observed visiting and collecting pollen at most sites, and their absence at others is probably due to lack of colonies in the area. *Brachypeplus* sp. and the staphylinid were always present, often immersed in the accumulated pollen of the spathal catchment area above the spathal constriction. However, no beetles were ever observed arriving or leaving and experiments on their vagility are necessary to determine their ability as pollinators. The small size of the thrips makes them unlikely pollinators despite their common occurrence, and like the beetles, their vagility is unknown.

Normally ubiquitous, the honeybee was only observed visiting on a single occasion, despite their presence on other flowers at all localities. The only other insects encountered apart from *N. inversa* (already mentioned) (Table 1) were the phalacrid and the unidentified weevil, both single individuals.

The numbers of *N. inversa* recorded in the sealed chambers (Table 5) confirms the report of McAlpine (1978) and Shaw *et al.* (1982) that they occurred only in rainforest. (It should be noted, however, that two adult *N. inversa* were found in two open chambers at two of the Mt Coot-tha sites (Table 1). This may indicate that the fly is now finding its way to this area, which has only been established for four years.) The few occasional insects recorded in the sealed chambers (Table 2) show a similar basic composition, though less extensive, to those recorded by Shaw *et al.* (1982, table 5).

In his studies on the pollination of *A. macrorrhiza* in the Illawarra District near Sydney, Hamilton (1898) recorded the beetle, *Brachypeplus murrayi* in the open chambers. He also made some observations not substantiated by us, viz., beetles feeding on liquid exuded by the pistils and beetles, becoming confined in sealed spathal

chambers, later burrowing their way out. We noted no such feeding habit, nor any perforated chambers.

Hamilton (1898) also observed an unidentified species of agaristid (Lepidoptera: Agaristidae) in open chambers and claimed that they aided in fertilization. Larvae of the agaristid *Cruria donovani* (Boisduval) were noted at all rainforest localities during our study, where they were often seen inside buds and open chambers feeding on stigmas and ovaries. However, as a single head contains sufficient tissue to allow a larva to reach maturity they are unlikely to be effective pollinators.

If indeed *A. macrorrhiza* is insect pollinated as suggested by this study, then *Brachyepplus* sp. and the staphylinid would appear to be the most likely candidates since they occur at all localities examined. While *N. inversa* and *T. carbonaria* might appear to be more likely to be effective in this role, their absence from some localities where good seed set occurred does not support this, or at least suggests that a number of pollinating agents are involved, and that a resolution requires further investigations.

#### *Emasculation/bagging experiment*

The results of the emasculation/bagging experiment given in Table 3 show that all heads rotted if no seed was set (except four with a few seeds only) and conversely, the only heads which matured were those where seed had set (other than the four exceptions).

The results in Tables 3–6 show that, as seed occurred (other than in seven heads) only in unbagged, non-emasculated heads (Treatments 6 and 7), *A. macrorrhiza* is not apomictic, because if it were, seed could have occurred in all heads, unless pseudogamic.

Mesh-bagging allowed seed set (18 seeds) in only two heads out of 36 (Table 4) and therefore wind pollination is probably unlikely as a general occurrence. The 18 seeds (set in 12 berries) may have resulted from chance wind-borne or self pollen.

Emasculation resulted in seed set (228 seeds) in four out of 39 heads, compared with 2669 seeds in 27 out of 83 non-emasculated heads including labelled controls (Table 4). The four emasculated heads which had some seed set were unbagged and could have been fertilized by wind- or insect-borne pollen. In the non-emasculated heads, only two seeds were set in one out of 34 heads in any imperviously-bagged head (paper or plastic) and only 18 seeds in two heads out of 19 in the mesh-bagged heads (Table 4); the two seeds may have been the result of self pollination while the 18 seeds may have resulted from self or chance wind pollination. Twenty-four of the unbagged, non-emasculated (labelled) controls (Treatment 6) set 2649 seeds against six heads which did not (Table 4); the non-seed set in these heads may have been due to lack of pollen at the time of stigma receptivity and/or lack of pollinating agent(s).

The results shown in Table 5 confirm data previously reported by Shaw *et al.* (1982) viz., that there is great variation in the numbers of seed set per head (in the present study from 1.5% to 99.3% in the 48 heads, all controls except two); that there is no relation between numbers of seed set and numbers of *N. inversa* recorded in the sealed chambers (which it is presumed reflects the numbers of ovipositing females in the open chambers) at the rainforest sites; that no *N. inversa* were recorded in the sealed chambers at the garden sites but despite this seed up to 88.3% was still set in garden site heads.

Table 6 shows the theoretically expected seed set figures deduced from the treatments applied in our experiment. The actual results, also shown in Table 6, most nearly approximate those of crossing with insect pollination with the attractant excised in the emasculated heads. Small differences from the theoretical results occurred in the emasculated unbagged heads, where four heads set 228 seeds (possibly insect or chance wind-borne pollination); in the imperviously-bagged non-emasculated heads, where

two seed set in one head (probably self pollen); and in the mesh-bagged non-emasculated heads, where 18 seeds set in two heads (possibly self or wind-borne pollen), whereas no seed was expected in any of these classes. Also, all control (labelled) heads were expected to set seed but six heads out of 24 did not, a situation also found in the unlabelled controls.

The results of the experiment therefore appear to indicate cross pollination by insects, with little attraction for the insects if the appendage/staminate portion of the spadix is removed.

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